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GROWTH AND REGENERATION RATES IN THINLY ENCRUSTING DEMOSPONGIAE FROM TEMPERATE WATERS

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ABSTRACT

Thinly encrusting species of subtidal sponge grow at slow but measurable rates over natural surfaces by lateral spreading. Of the eleven species studied here, *Aplysilla rosea* had the highest undisturbed rate of growth and *Microciona* sp. the lowest with an overall negative change in size. Using the mean growth rate it can be estimated that the largest sponge patches observed in the field may be over seventy years old. Growth rates of individual patches were varied but this variation was not synchronous within a species nor did it show any regular temporal pattern. Similarly, no relation between the normal thickness of the species, the wet weight, or true organic content of the species with undisturbed rates of growth could be found. However, the mean patch size of the species was correlated with the undisturbed growth rates. If the tissues of the sponges were damaged, rapid regeneration was initiated at rates many times greater than the undisturbed growth rate of the species. It was also found that even very small sponge patches could recover after almost all living tissue was scraped from the rock.

INTRODUCTION

Almost no data exists on the rates of growth and regeneration, or estimates of the age of, thinly encrusting species of marine sponge. Similarly, little information is available for other invertebrate groups with a sheet-like growth form such as compound ascidians, crustose bryozoans and corals (Jackson, 1979). It is thought that growth in these types of sessile organisms is indeterminant, the colony increasing exponentially in size with time (Jackson, 1977). From studies of sponge explant outgrowths it has been shown that the tissue initially spread out is undifferentiated and only slowly thickens and develops functional units (Simpson, 1963). The rate of growth in subtidal thinly encrusting sponges is apparently slow. Bryan (1973) studying a tropical species of *Terpios* over several weeks found that it could grow over unoccupied space at a rate of 0–0.02 mm^2/cm border/day but this rate increased to 0.08–0.10 mm^2/cm border/day when the sponge grew over living coral. In a temperate water community A. M. Ayling (1981) found over a month's study period that *Stylopus* sp. grew at an undisturbed mean rate of increase of 0.02 mm^2/cm border/day.

The growth of intertidal sponges (usually of thickly encrusting habit) has been studied in a little more detail. Although these species are not directly relatable to the subtidal thinly encrusting forms because of their seasonal life history modifications (see Fell, 1976), some of the features of their actual growth are pertinant. Fell and Lewandrowski (1981) found that the smallest and largest sponge patches of *Halichondria* sp. grew the most slowly. Patches of these sponges could also merge

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and disintegrate (Elvin, 1976; Johnson, 1978; Fell and Lewandrowski, 1981), a feature also observed in corals (Hughes and Jackson, 1980). The rates of such fission and fusion processes may have an important bearing on estimates of age in these organisms.

A. M. Ayling (1981) found that when the thinly encrusting sponge *Stylopus* sp. was damaged in an experiment simulating the effects of urchin grazing, the sponge tissues regained lost space at a rate 200 times the normal growth rate of the species. This regeneration rate refers to the formation of a thin layer of tissue over the lost space, not to the production of the normal thickness of the species. The large difference between growth and regeneration rates may help explain the abundance of thinly encrusting forms of sponges in areas subject to grazing and other disturbances (Jackson and Palumbi, 1978; A. M. Ayling, 1981). The high 'growth' rates attributed to sponges in recolonization experiments (Kay and Keough, 1981) may also involve this regeneration process. Other examples of regeneration rates reported by A. M. Ayling (1981) range from 1.6 mm^2/cm border/day for *Tedania* sp. (orange) to 4.0 mm^2/cm border/day for *Anchinoe* sp. (yellow).

This paper provides growth rates for eleven species of thinly encrusting subtidal sponge taken from two years monitoring of sponge patches in the natural habitat. From these data estimates of longevity were derived. Data were also collected on wet and dry weights and true organic content and related to the growth rate. Similarly, the effect of seasonal and reproductive state of the sponges on growth rates is considered. The regeneration rates of the sponges were experimentally determined and the ability of small sponges to survive damage also investigated.

Materials and Methods

Description of study area

With the exception of one species, all the thinly encrusting sponges were located on the walls of a narrow canyon, 12 m in depth, on the exposed north-easterly side of Goat Island, a small island near the Leigh Marine Laboratory off the north coast of New Zealand (38° 16'S: 174° 48'E). The other species, *Eurypon* sp., was found only in the Sponge Garden at a depth of 18 m north-west of Goat Island. This species was abundant beneath a layer of sand between 2 and 5 cm in depth. The physical characteristics of the Goat Island area are summarized in Leum and Choat (1980) and A. M. Ayling (1981). The abundance of the sponges is given in A. L. Ayling (1978).

Wet weight, dry weight, and composition of living sponges

Five or more pieces of each species were collected still attached to the rock substratum and transferred to the laboratory where the area of the sponge was traced onto acetate sheet and thickness measured. The tissues were then carefully removed with a scalpel and paint brush, placed on filter paper and weighed. Sponges were placed in a drying oven at 90°C until constant weight was obtained. A wet weight/dry weight ratio was calculated and the dried residue of the sponge further examined for ash (assumed to be all SiO_2 for siliceous sponges), water of hydration and organic fractions. At normal drying temperatures (80–100°C) the water of hydration is only partly removed from the siliceous skeleton. As ash values can thus be underestimated (Vinogradov, 1953; Paine, 1964) corrections were made by measuring the weight loss of spicule samples after incineration. Spicule samples were collected from two species. Tissue samples from the two species were digested in Sodium hydroxide and then repeatedly washed in distilled water. Cleared spicules were dried at 90°C, weighed and incinerated at 500°C for four hours. All species were ashed at 500°C for four hours.

Growth rates of sponges over natural habitat

Ten or more patches of varying sizes of each encrusting species were selected and marked with labeled masonry nails driven into the rock adjacent to the sponge patch. At the end of the study only those patches which had not suffered visible damage from grazing or other sources of disturbance were chosen for estimating growth rates. It is possible that some of these 'undamaged' sponges may have suffered minor injuries and regenerated between monitoring intervals. Preliminary monitoring of growth at weekly then monthly intervals showed no measurable changes in size in most of the species and hence monitoring was continued at three monthly intervals over a two year period (June, 1976–June, 1978). Sponge patches were photographed and the color negatives projected at actual size onto graph paper and the outlines of the sponge traced. The area cover of each sponge was recorded with an estimated error of ±0.5%.

Damage simulation experiments

A ten centimeter square was outlined on the surface of the sponge and then scraped almost clean of tissue to simulate the grazing activities of the abundant urchin *Evechinus chloroticus*. Five sponge patches of each species were then cleared and black and white photographs were taken of the damaged areas. Cleared areas were rephotographed a month later and percentage regeneration measured.

Can small sponges survive damage?

The recovery capability of small sponges was investigated by scraping patches of between 0.1–42.0 cm^2 area of the species *Microciona* sp. and *Stylopus* sp. almost completely off the rock. After two weeks the percentage recovery of the original area was recorded.

RESULTS

Wet weight, dry weight and composition of living sponges

Wet weight and dry weight per unit area of the sponge is shown in Table I. The species with the highest wet weight per centimeter square tissue were *Tedania* sp. (orange) and *Hymedesmia* sp. (orange). The high wet weight of *Chondropsis* sp. is due to the inclusion of sand in its skeleton.

A wet/dry weight ratio was calculated and the ash, water of hydration and the organic fractions of each species obtained (Table II). Results from this analysis indicate that the species with the least proportion of organic matter in their body include species where spongin forms a major part of the skeleton (*Chelonaplysilla* sp.), or sediments (*Chondropsis* sp.) or the sponge produced large quantities of mucus (*Tedania* sp. (orange)). In general these temperate water encrusting sponges had a greater proportion of organic matter, but less water content than the species from Antarctica analyzed by Dayton *et al.* (1974).

TABLE I

Thickness, mean patch size, wet weight, and dry weight of thinly encrusting sponges

Species	No. samples	Thickness (mm)	Mean patch size (cm^2) area	Wet weight g/cm^2 tissue $\bar{X}$	Wet weight g/cm^2 tissue $S\bar{x}$	Dry weight g/cm^2 tissue $\bar{X}$	Dry weight g/cm^2 tissue $S\bar{x}$
Stylopus sp.	6	3–10	58.4	0.16	0.06	0.05	0.02
Hymedesmia sp. (orange)	5	5	8.2	0.19	0.08	0.08	0.04
Hymedesmia sp. (red)	8	2	13.6	0.14	0.02	0.09	0.03
Microciona sp.	14	3	22.2	0.07	0.01	0.03	0.004
Anchinoe sp.	5	2–15	21.9	0.06	0.01	0.03	0.01
Stylopus sp. (pink)	10	2–5	30.7	0.13	0.08	0.02	0.003
Tedania sp. (orange)	7	5–15	14.5	0.19	0.04	0.04	0.01
Chondropsis sp.	16	5–20	45.8	0.37	0.03	0.16	0.01
Aplysilla rosea	7	2–6	151.8	0.09	0.02	0.04	0.01
Chelonaplysilla sp.	7	3–5	83.8	0.09	0.02	0.05	0.01
Eurypon sp.	10	1–2	7.8	0.03	0.003	0.02	0.01

Natural growth rates

The thinly encrusting sponges grew in slow but measurable increments over the two year study period. In the majority of cases this growth was not a steady uninterrupted process; during a year a single sponge patch could stop growing or retract from areas it had occupied. Whether this retraction was spontaneous or due to

TABLE II

*Composition of living sponges**

Species	N_1	A Proportion H_2O ± SE	B Proportion dry (1.000 − A)	N_2	C Proportion of dry wt. that is false ash ± SE	D Proportion true ash B × C/0.91	E Proportion true organic matter (B–D)
Stylopus sp.	6	.695 ± .026	.305	5	.645 ± .047	.196	.109
Hymedesmia sp. (red)	8	.502 ± .030	.498	5	.327 ± .066	.115	.383
Hymedesmia sp. (orange)	5	.664 ± .058	.335	5	.569 ± .017	.209	.126
Stylopus sp. (pink)	10	.560 ± .174	.440	5	.454 ± .017	.219	.221
Tedania sp. (orange)	7	.787 ± .014	.213	5	.710 ± .061	.166	.047
Microciona sp.	14	.544 ± .033	.456	5	.581 ± .011	.201	.165
Anchinoe sp.	5	.457 ± .180	.643	5	.409 ± .021	.289	.354
Chondropsis sp.	16	.564 ± .010	.436	5	.692 ± .160	.414**	.022
Chelonaplysilla sp.***	7	.425 ± .070	.550	5	.938 ± .043	.516	.034
*Aplysilla rosea****	7	.542 ± .075	.458	5	.418 ± .023	.191	.267
Eurypon sp.	5	.716 ± .041	.783	—	—	—	—

* N_1 = number specimens used for determination of proportion H_2O (A); N_2 = number of specimens used for determination of proportion of false ash (C). True ash is false ash/0.91 − water held by spicules. The composition of sponges is given by (A) = (D) + (E).

** True ash is false ash/0.729 − sand and spicules.

*** Sponges without spicules, true ash (B) (C).

undetected disturbance could not be determined in this study. When individual changes in patch size were graphed no correspondence in fluctuations were apparent or referrable to seasonal or reproductive cycles (see A. L. Ayling, 1980 for the reproductive cycles of four of the species studied here).

A mean growth rate was calculated for each species of sponge, the large standard errors reflecting the above mentioned fluctuations in size. Growth rates are presented as millimeter square area change in size per centimeter border per day in Table III. Patches of *Aplysilla rosea, Stylopus* sp. (pink) and *Chondropsis* sp. grew relatively rapidly at 0.28, 0.23, and 0.13 mm^2/cm border/day respectively. It is estimated that a *Stylopus* sp. (pink) of one centimeter diameter growing undisturbed could reach a size of 15 cm diameter in ten years and the larger patches of this species observed on the walls of the canyon which were one meter in diameter may be 78 years old (based on the mean growth rate shown in Table III). If grazing was more frequent than detected then these estimates of longevity should be considered minimum age estimates. *Eurypon* sp. grew the most slowly of all the sponges, and patches of this species were easily recognized even after six and a half years as the outlines of the sponges changed very little (Fig. 1).

No significant relationship was found using the Spearman Rank Correlation coefficient r_s between wet weight and growth rates ($r_s = 0.52$), thickness and growth rates ($r_s = 0.508$) or true organic content and growth rates ($r_s = 0.167$). However, a significant correlation was found between the mean patch size of a species and growth rates ($r_s = 0.64$: $0.5 > P > 0.01$). Thus, in general, large species such as *Aplysilla rosea* and *Chelonaplysilla* sp. grew more rapidly than the smaller species *e.g., Hymedesmia* sp. (orange) and *Eurypon* sp.

The smaller sponges were more likely to fluctuate in size than the large individuals. This is shown for six of the species in initial size-increment graphs in Figure 2.

Effect of grazing on sponges (regeneration rates)

The regeneration rates of the sponges are shown in Table IV. Sponges could regenerate into disturbed areas at rates 22 to 2,900 times the natural growth rate.

TABLE III

Growth rates of thinly encrusting sponges over natural habitat

Species	Number patches	mm^2/cm border/day $\bar{X}$	mm^2/cm border/day $S\bar{x}$	Postulated diameter of a 10 yr old sponge using mean rate of increase (cm)
Aplysilla rosea	3	0.28	0.19	20.03
Stylopus sp. (pink)	11	0.23	0.09	15.39
Chondropsis sp.	16	0.13	0.09	9.31
Tedania sp. (orange)	22	0.08	0.05	5.70
Stylopus sp.	12	0.08	0.06	5.71
Chelonaplysilla sp.	13	0.06	0.05	5.00
Hymedesmia sp. (red)	10	0.05	0.03	4.31
Hymedesmia sp. (orange)	5	0.02	0.03	2.32
Anchinoe sp.	9	0.01	0.06	1.66
Microciona sp.	25	−0.01	0.003	—
Eurypon sp.	9	0.0003	0.031	1.02

Growth rates are presented as mean growth over a two year period.

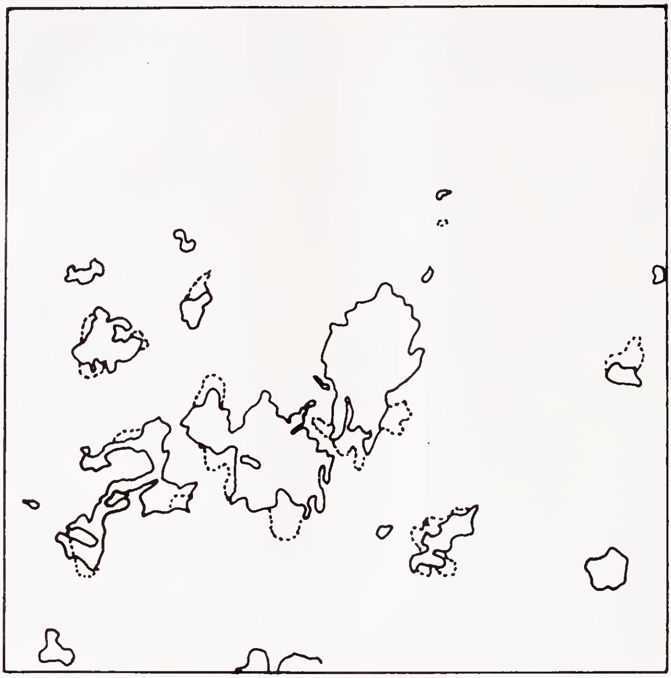

FIGURE 1. Changes in outlines of patches of *Eurypon* sp. taken from color photographs over the period June, 1975 (——) to February, 1982 (- - -) in a 25 cm^2 area of the Sponge Garden.

The tissue covering these disturbed areas is initially thinner than the normal thickness of the species. The species that most rapidly recovered space after damage were *Stylopus* sp. (pink), *Aplysilla rosea, Chondropsis* sp, and *Stylopus* sp. However the greatest magnitude of difference between growth and regeneration rates occurred in the slow growing species *Eurypon* sp. and *Anchinoe* sp. Using the Spearman Rank Correlation coefficient some relationship was found between regeneration rates and undisturbed growth rates ($r_s = 0.91$; $P < 0.01$) and regeneration rates and the mean patch size of the species ($r_s = 0.64$; $0.5 > P > 0.1$).

Can small sponges survive damage?

All patches of the rapidly growing species, *Stylopus* sp. reoccupied some of the lost space, the smallest patches recovering all of their former space in less than two weeks. In some cases however, the slower growing species, *Microciona* sp. did not recover any space nor the entire area even over a month (Fig. 3).

DISCUSSION

Growth over natural surfaces in thinly encrusting sponges from temperate subtidal waters is very slow. The most rapid mean rate of growth recorded in this study was that of a thin fleshy sponge, *Aplysilla rosea,* at 0.28 mm^2/cm border/day. A settled larvae of this species growing undisturbed could reach a size of 20 cm diameter in ten years based on this mean rate of growth. Some of the patches of this species growing on the walls of the canyon reached a meter diameter and these could be a minimum of 50 years old. The slowest growing species was *Eurypon* sp., growing at

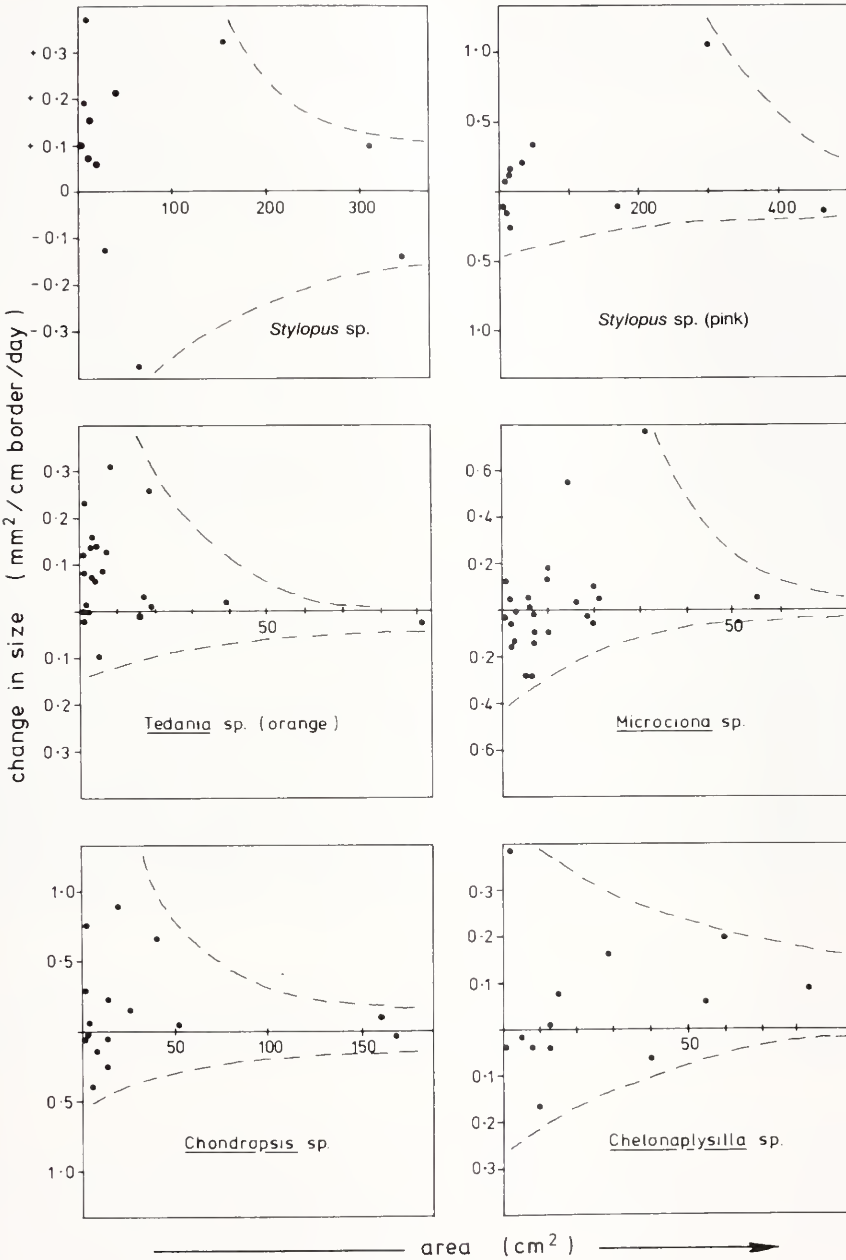

FIGURE 2. Initial size-increment graphs of thinly encrusting sponges showing how small patches generally fluctuated more in size than larger patches. Dashed lines outline the areas where there are no points.

a mean rate of 0.0003 mm^2/cm border/day. In ten years the settled larvae of this species would only grow to a size of one centimeter diameter. This species is very thin and in the natural habitat forms small patches up to 10 cm in diameter, the

TABLE IV

*Regeneration rates of thinly encrusting sponges**

Species	mm²/cm border/day $\bar{X}$	$S\bar{x}$	Times magnitude greater than the natural growth rate
Aplysilla rosea	6.18	0.98	22.07
Stylopus sp. (pink)	6.98	0.78	30.35
Chondropsis sp.	5.70	0.83	43.85
Tedania sp. (orange)	4.18	1.34	52.25
Stylopus sp.	4.60	0.70	65.70
Chelonaplysilla sp.	4.08	1.20	68.00
Hymedesmia sp. (orange)	0.53	0.43	26.50
Anchinoe sp.	3.65	0.89	365.00
Microciona sp.	0.63	0.23	—**
Eurypon sp.	0.88	0.44	2,900

* Regeneration rates were obtained by stimulating damage to the sponge, five replicate simulations per species. *Hymedesmia* sp. (red) is not included in the table as it was too small and divaricate to use in the experiment.

** Undisturbed growth in this sponge was negative over the period of study.

outlines of which change very little over long periods of time. *Microciona* sp. had an overall negative growth rate although the positively growing individuals of this species achieved a growth rate of 0.02 mm^2/cm border/day.

Every species had some individual patches which regressed over the two year study period. In some cases the patch could increase over several months then decrease in size. As fluctuations in size did not occur contemporaneously between individuals no relationship could be found between changes in size and seasonal and reproductive cycles. Changes in size did not occur over the entire border line of the sponges but were restricted to certain sections of the border. Thus while sections of the border could remain unchanged during the study other sections could

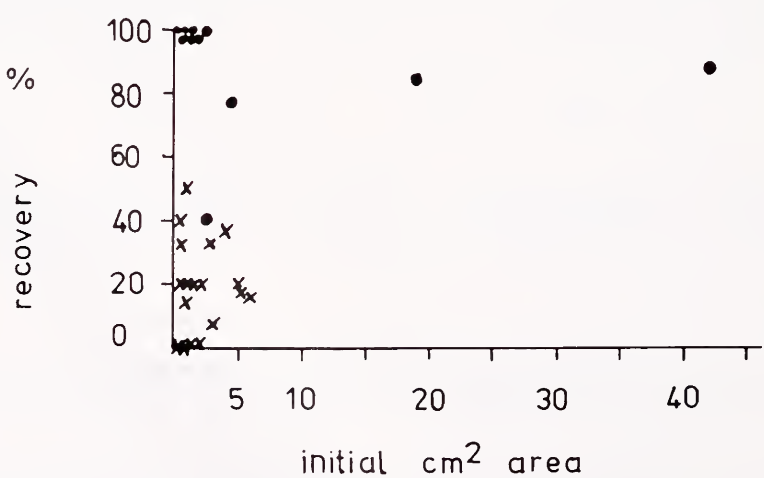

FIGURE 3. Can small sponges survive damage? Sponges were scraped almost entirely off the rock and recovery of space was recorded after two weeks time. × = *Microciona* sp.; ● = *Stylopus* sp.

expand outwards or contract inwards. Neighboring sponges may help maintain static border outlines and explain some tissue retractions (A. L. Ayling, in press) but whether the removal of surrounding invertebrates may stimulate growth is uncertain (A. M. Ayling, 1981).

The longevity of these thinly encrusting sponges may not be estimated correctly if only the mean rate of increase is considered. Like corals (Hughes and Jackson, 1980) and intertidal sponges (Elvin, 1976; Fell and Lewandrowski, 1981), these subtidal sponges could be broken into several fragments some of which may later join. Thus a single patch may be the result of several fissions and fusions over time, and the size of the sponge may not be indicative of the age of the patch. In general these thinly encrusting sponges are likely to occupy space in the community for long periods of time and consequently would be expected to play an important part in the structuring of these encrusting communities where they are abundant.

The sponge species' tissue thickness did not affect the rate at which the sponge grew over the substratum. For example, the thinnest sponge, *Eurypon* sp. grew the slowest, while the thickest species *Chondropsis* sp. grew relatively rapidly. Nor did the undisturbed growth rate of the different species relate to the wet weight or true organic content. However, it was found that the larger species grew more rapidly than the smaller species.

When thinly encrusting sponges are damaged a rapid regeneration mechanism is activated and the sponge spreads out a thin layer of tissue over the disturbed area, regaining the lost space. This thin tissue may be similar to the explant tissue examined by Simpson (1963) which was undifferentiated and contained only a few cell types. The highest rate of regeneration recorded in the present study was that of *Stylopus* sp. (pink) at 6.98 mm^2/cm border/day, a magnitude of 30 times greater than the undisturbed growth rate of the species. Even the slowest growing species, *Eurypon* sp., rapidly regenerated tissue at a rate of 0.88 mm^2/cm border/day, a magnitude of 2,900 times the undisturbed growth rate of the species. This rapid rate of encroachment after damage has obvious advantages in communities where grazers are abundant. The survival chances of newly recruited sponges would also be enhanced by this regeneration mechanism.

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